

The influence of food supply on the population dynamics of rabbits, *Oryctolagus cuniculus* (L.), in a Dutch dune area

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Abstract

The population dynamics of rabbits in a temperate, maritime climate were studied in response to the question: are rabbit numbers kept in check by intrinsic responses to density, or by predation and disease, or do they rise to the level permitted by the food supply? The study was carried out in a few small observation plots within a coastal dune nature reserve. An experiment employing supplemental feeding was conducted during autumn and winter. In the severe winter of 1978–79 rabbits died from starvation. In the following years population density increased, but did not reach the upper limit set by food availability. Fullgrown rabbits were eaten by fox, stoat and occasionally cat and polecat. Littering frequency was low and may have been depressed by high rabbit density. The length of the breeding season was determined by an interaction between population density and food quality. Predation and other mechanisms potentially capable of regulating population size were not strong enough to keep rabbit density below the level permitted by the food supply. Reasons for this are discussed.

Introduction

In the coastal sand dunes of the Netherlands many nature reserves are established. The vegetation is vulnerable to overgrazing, which can lead to rain and wind erosion. Rabbits can cause severe damage to dune vegetation, and in many places managers try to control rabbit populations by hunting them during autumn and winter. The question remains, however, whether availability of food during the winter already limits rabbit population densities. This question has become more of present interest since the impact of myxomatosis is lessening.

It has been discussed widely as to whether herbivore numbers are limited by food supply, or whether intrinsic behavioural responses to high density, or predation or disease, prevent populations from reaching the limit set by food availability.

WATSON and MOSS (1970) argued that since changes in behaviour (dominance, spacing behaviour and aggression) invariably attend population limitation, these factors must be all-important in setting population size. However, it is more likely that changes in behaviour arise as inevitable symptoms of cover-crowding displayed as the carrying capacity of the habitat is reached (e. g. LACK 1954).

COWAN and GARSON (1985) describe how rabbit numbers are limited by the number of burrows on the chalk, but not on the dunes. On the chalk, much more aggression and burrow defence occurred.

GIBB et al. (1978) considered that density-dependent behavioural or physiological mechanisms were too weak to regulate populations of rabbits. They stated that “the population of rabbits appeared to be limited by extrinsic factors alone” and concluded that rabbit populations in New Zealand were kept in check by predators, mainly feral cats and ferrets.

Rabbits have been particularly well studied in Australia. MYERS and POOLE (1963) concluded that starvation was the only mortality factor of consequence in determining density. MYERS (1971) forwards the hypothesis that the characteristics of rabbit population

dynamics in Australia reflect the conditions under which the rabbit originally evolved: "The rabbit in Australia possesses no inbuilt physiological or behavioural mechanism to control its numbers. The rabbit evolved in a system where extrinsic mortality factors (mainly predation) are necessary to maintain population stability."

The rabbit evolved in the Mediterranean region (FLUX and FULLAGAR 1983), and so, according to MYERS, rabbit numbers there should be kept in check by predation.

Compared with the relatively recent introductions of rabbits in Australia and New Zealand, rabbits have been established in north-western Europe since 1250 (RENTENAAR 1978; VAN DER FEEN 1963). Predation might be expected to have a greater impact on rabbit numbers in these older habitats. However, with regard to predation, the situation in north-west Europe is quite different from that in the Mediterranean. DELIBES and HIRALDO (1981) describe that in Spain many more birds of prey and mammalian predators prey on rabbits than in other parts of Europe.

Historically, foxes, cats, mustelids and birds of prey have been much hunted in the dutch coastal dunes, to protect hunting and commercial interests in rabbits. Predators are protected now, and the fox has re-established itself since 1968. This fact led to this study on the population dynamics of rabbits.

The study was set up to determine whether rabbit numbers rise to the level permitted by their food supply.

It is impossible to quantify food supply correctly. Standing vegetation is not the same as available food. Only part of the vegetation is usable, so suitable food can be in short supply even where vegetation is abundant (SINCLAIR 1975). In addition, rabbit grazing can effect the composition of vegetation and hence the suitability of the habitat, and plants may show compensatory growth in response to grazing (McNaughton 1983).

Therefore, to determine whether rabbit numbers have reached the level set by the food supply, we studied whether reproduction and survival are food-dependent.

A few small populations were monitored by catching, marking and observing over several years. By providing supplementary food to one population it could be determined whether relieving food scarcity in wintertime led to reduced mortality and an increase in reproduction.

This experimental approach was supplemented by a study on condition and diseases of rabbits shot in other parts of that same dune reserve (WALLAGE-DREES 1986).

Observations on rabbit breeding in stops was done on a former arable field used as parking lot in the same dune reserve.

Methods

The study area

The study was carried out between January 1978 and June 1981 in the 'Noord-Hollands Duinreservaat' (NHD), and area covering 4765 ha of coastal dunes northwest of Amsterdam. The reserve is managed by the Provincial Waterworks of North-Holland (PWN), and rabbits are hunted by game wardens in order to reduce damage. With their help many data on condition and food of rabbits were collected (WALLAGE-DREES 1986; WALLAGE-DREES and DEINUM 1986).

The actual study area was situated about 800 m from the sea in a vegetation mosaic of *Hippophaë rhamnoides*, *Rubus caesius*, *Salix repens*, mosses, forbs, grasses and sedges (mainly *Festuca ovina*, *Carex repens*) classified as '*Rubus caesius* landscape' (DOING 1964).

This coastal area has a mild, maritime climate (fig. 1) with little seasonal fluctuation in rainfall. There is usually some snow in January and February. The first study winter in 1979 was much colder than average; snow covered the ground completely for 23 days in January and February and there were at least 5 days with glazed frost.

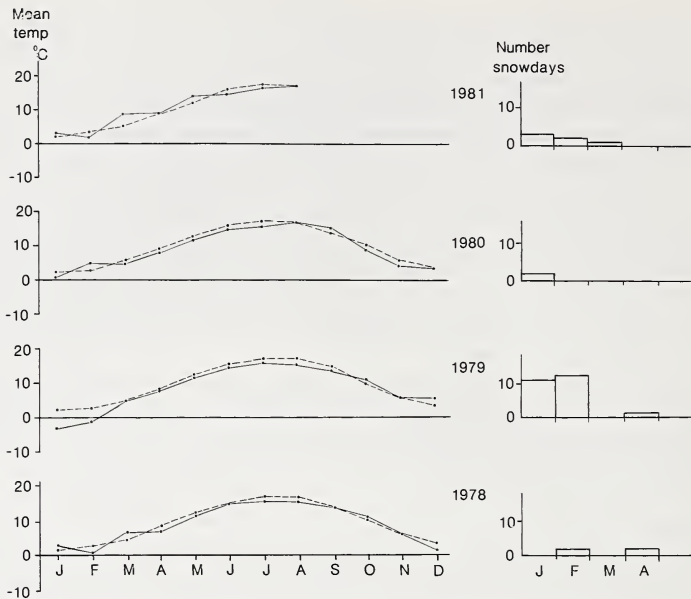


Fig. 1. Left: Monthly temperature means in °C (—) together with the means over 1950–1980 (---). Data from KNMI, De Bilt. – Right: Number of days with complete snow cover. Data from the recording station of PWN at Castricum

The observed populations

Rabbits were observed in seven plots (table 1). Five plots were made by fencing in a few inhabited burrow systems, including foraging areas, while the sixth and seventh populations were left as unfenced controls. Plot 7 was added in 1980 and was bounded on two sides by a canal, on a third side by high grass not used by the rabbits and was open on the fourth side.

The boundaries of plots 6 and 7 were determined from observations on the movements of the rabbits that lived inside the plots.

The size of our plots varied from 0.7 to 1.4 ha (table 1). MYERS (1964) did not notice any detrimental effect on behaviour or physiology when keeping rabbits in enclosures of 0.3 and 0.7 ha.

Fences were 1 m high with a mesh width of 3 cm. They were designed to ensure which rabbits got the supplemental food, while (as far as possible) allowing free access to predators.

Table 1. Size of the plots in the study area

Fenced			Unfenced		
No.	Size	In use	No.	Size	In use
1	1.3 ha	1978–79	6	1.3 ha	1978–79
2	0.7 ha	1978–79, 1980–81	7	1.4 ha	1979–81
3	0.7 ha	1978–79			
4	1.3 ha	1978–79			
5 ¹	1.4 ha	1978–79, 1980–81			

¹ Plot with supplementary feeding.

The drawback of fencing was that it prevented dispersal. However, dispersal in rabbits is generally found to be small and not responsible for regulating population density (GIBB 1977; MYERS and POOLE 1961; MYERS and SCHNEIDER 1964; MYKYTOWYCZ and GAMBALE 1965; SOUTHERN 1940; TYNDALE-BISCOE and WILLIAMS 1955). We never noticed immigration of untagged rabbits into our unfenced populations and consequently, also considered that there was no emigration. This was

corroborated by the fact that no tagged rabbits from the observed populations were seen or shot outside the study area. Also, from rabbits tagged as nest young on the parking lot, 5 out of 45 were shot in their first year, all not farther than the border of the parking lot.

We believe that fences did not significantly influence predator activity. The main predators in the coastal dunes were stoat, polecat, fox and feral cat. Both stoat and polecat could creep through the fence and cats and foxes could climb over it. From tracks and sightings we know that stoats, polecats and foxes got inside the fences.

The fences possibly increased the chance of predation by making escape more difficult. This could only be checked for predation by stoats. Predation by a stoat can be recognized from bite-wounds on the rear of the animal (only visible by removing the fur), a gaping wound in the neck, and extensive subcutaneous haemorrhage (HEWSON and HEALING 1971). The fenced plots and another similar area of the same size (5.4 ha) were searched for rabbit carcasses. Between 1 November 1978 and 1 March 79, 14 carcasses/ha were found in the fenced areas and the same number in the searched area. Therefore, assuming the same population density on both sites, fences do not seem to have influenced the level of mortality caused by stoats.

Parameters of survival and reproduction

Two sets of parameters were measured. Population size in autumn and winter, impact of predation, body weight in wintertime were assessed with regard to rabbit survival and litter size, timing of the breeding season, littering rate, growth and survival of the young, the relative participation of adult and juvenile females in breeding were assessed with regard to reproduction.

Supplemental feeding experiment

To determine the influence of food availability on winter mortality an experiment was conducted in which the rabbits in plot no. 5 were supplied with additional food. This consisted of oats, wheat and the peel of *Ceratonia siliqua*, producing a mixture of high energy and low protein. Food was scattered ad libitum every two days at three foraging spots from 21 October 1980 until 20 March 1981. The food remained in good condition for at least two days. If little food was left over, the amount supplied was increased. Initially, 2.25 kg was given at each feed, which was increased to 4.5 kg from December onwards.

Condition of rabbits and population size

Rabbits were caught in live traps baited with oats and set at foraging spots. A few were caught by ferreting. After capture weight, sex and length of the hindfoot were recorded. Because rabbits were released we used body weight to distinguish juvenile (first-year) and adult rabbits. In shot rabbits from the same reserve body weight correlated well with eye lens weight, which is regarded as a reliable parameter of age (WALLAGE-DREES 1986). To determine whether females were pregnant and/or suckling, the condition of the nipples and the fur on the belly were checked (females line the nest with fur shortly before parturition) and the belly palpated. At first capture, rabbits were marked on both ears with a label that could be recognized at day or night when observing with a telescope: a monel wing band size 4 with an enlarged surface covered with reflecting yellow tape and with an individual code in black letters and numbers.

Two methods were used for estimating population size:

- a. Field counts were made just after sunset. The highest value of four counts on consecutive days was divided by the maximum proportion that was above ground in the same area during that month (WALLAGE-DREES 1988).
- b. From September 1979 onwards, when the major part of the population had been marked, live-catchers were constructed from recaptures and sighting. The number of unmarked individuals was assessed from sightings.

Population size was not calculated using a capture-recapture method, however, because the chances of being caught were not randomly distributed (DALY 1981; this paper table 2).

The whole observation area was searched intensively during the study and the chances of having missed emergent litters or fullgrown rabbits with severe myxomatosis were low. Also, the game wardens were aware of our study and brought us tags or tagged rabbits whenever they found them.

Recruitment and juvenile survival

Young rabbits are born in a nest-chamber, either in a blind diverticulum of a warren system or at the end of a separate blind tunnel called a 'stop' (LLOYD and COWAN 1968). The doe visits the young only once or twice during 24 hours and leaves the nesting burrow blocked up while she is absent. Young

rabbits emerge and make small excursions outside the burrow from about their 22nd day (BROEKHUIZEN *et al.* 1986). From that age onward they could be caught in traps set in the burrow entrance. The probability of capturing them was increased by finding the places where young emerged. Older young were also caught in traps set at foraging spots. Young were marked with the same tags as the adults.

The populations under observation littered in existing burrows. Many nests appeared to be located in empty burrows of which there were large numbers.

Stops were found on former arable fields in the reserve, which are now used as parking lots or as playgrounds. Nests in stops provided data on litter size and growth of kittens that could not be obtained from the actual study area.

Litter size is affected by the partial loss of embryos during gestation (BRAMBELL 1943) and by the death of part of the litter in the nest. One has to be careful in opening a stop lest the doe deserts the young. We found that stops with young under 10 days, even when opened carefully and blocked again after inspection, were deserted by the mother. The birth date was estimated from the timing of visits by the doe: once the young are born she opens the stop every night (MYERS 1958). Litter size was defined as the size at the first count 10 days after the birth of the litter.

In 1980 and '81 not enough stops were found to determine litter size from nests in stops. However, in 1981, the litter size in utero from rabbits shot in February and March could be recorded when uterine swellings were visible at dissection. The embryos were aged according to the drawings of MINOT and TAYLOR (1905).

Littering rate

The littering rate is the number of litters born each month divided by the number of adult females present at the beginning of the next month (PARER 1977). In this study the number of litters per year per doe was assessed by observation and capture of emergent young.

Rabbits have a post-partum oestrus. In this study littering rate was never 100 %. No distinction could be made between does that did not conceive post-partum, lost embryos before full-term, or whose young did not survive till emergence.

Pattern of the breeding season

The pattern of the breeding season was deduced from the appearance of litters in the study area and the distribution of age cohorts in the autumn bag of the wardens.

The age of dead rabbits

The age of dead rabbits was determined using their eyelens weight according to the formula given by MYERS and GILBERT (1968), i. e. age (days) = $-57 + 181.4/\ln(314/\text{lens weight [mg]})$. A similar formula was found in this study, based on data from 15 rabbits with known birth date who were either shot at the parking lot or found dead in the study area. This sample gave: age (days) = $-64 + 228.8/\ln(314/\text{lens weight [mg]})$ which lies within the 11 % standard deviation given by MYERS and GILBERT (1968). As their formula was based on a much larger sample, it was used.

Available food in the breeding season

To assess the quantity and quality of food available during the breeding season, the relative biomass of the vegetation was measured from mid-February to mid-June. The relative biomass of a 'species' was defined as the product of cover and average height. Cover was measured by the point-quadrat method (MUELLER-DOMBOIS and ELLENBERG 1974) and average height by measuring all plants touching the point quadrat within a distance of 0.5 cm. This was done on a grid of 392 points. Cover was summed and height averaged for monocotyledons and dicotyledons separately, as these show a difference in quality as rabbit food (WALLAGE-DREES 1983).

Results

Winter mortality

Capture rate

Captures in the baited live-traps were not distributed at random with regard to age and sex. For example, table 2 gives figures for a few months in which the composition of the population was well-known. In autumn juveniles were caught more often than adults (2A), pregnant does were caught more often than bucks (2B) and supplementary feeding reduced the chance of capture (2C). In September, juveniles increased in weight more than adults (table 7), and does need extra food when pregnant or lactating. Generally, one might conclude that rabbits which need more food enter the traps more readily.

Table 2. Capture rates

A Frequency of captures of adults and juveniles plot 2 and 7						
	September 1980			January 1981		
	n	captures	χ^2	n	captures	χ^2
Adults	36	3	85.3 ($p < 0.001$)	8	6	0.76 n.s.
Juveniles	12	33		17	8	
B Frequency of captures of ♂♂ or ♀♀ in the reproductive season (1 March–3 June) 1981, plots 2, 5 and 7						
	n	captures	χ^2			
♂♂	14	17	11.9 ($p < 0.001$)			
♀♀	18	55				
C Frequency of captures in plot 5 with supplementary feeding, compared with the untreated plots 2 and 7 (January 1981)						
	n	captures	χ^2			
Plot 5	16	3	3.3 n.s.			
Plots 2 and 7	25	14				

Tested: observed vs. expected values.
n = population size.

Population reduction

Table 3 gives the number of rabbits in the plots and the mortality rate during autumn and winter. A variable number of plots were used, because, following heavy mortality in the winter of 1978–79, not enough rabbits survived in the original study area to continue the work there. Consequently, we moved to another area nearby called plot 7. Meanwhile, plots 2 and 5 were restocked with rabbits caught in other parts of the reserve, and so plots 2, 5 and 7 could be monitored in 1980–81. The mortality rate varied between months and years. It was highest from December 1978 to March 1979. In 1980–81 no differences in mortality rate were found between plot 5, with supplemental feeding, and the controls.

For 1979–80 and 1980–81 the mortality of juveniles and adults and of the two sexes were calculated separately. No significant differences were found, either between age-groups or sexes, and therefore, these classes are not treated separately in table 3.

Table 3. Population size and mortality in the study areas

	Population size			Mortality (%)	
	Sept.	Dec.	March	Sept.-Dec	Dec.-March
1978-'79					
Plot 1-6 6.7 ha	244	89	25	64	72
1979-'80					
Plot 7 1.4 ha	41	32	21	22	34
1980-'81					
Plots 2 and 7 2.1 ha	48	29	19	40	34
Plots 5 ¹ 1.4 ha	29	21	12	28	43
Population decrease 1978-79 vs. 1979-80: $\chi^2 = 40.6$ $p < 0.001$					
1980-81: $\chi^2 = 24.7$ $p < 0.001$					
Population decrease 1979-80 vs. 1980-81: $\chi^2 = 0.79$ n.s.					
1980-81, in autumn, plot 5 vs. plot 2 and 7: $\chi^2 = 0.68$ n.s.					
1980-81, in winter, plot 5 vs. plot 2 and 7: $\chi^2 = 0.09$ n.s.					
¹ Experimental plot: supplemental feeding during October to March.					

Causes of death

In table 4 data about the causes of death are summarized and compared to the decrease in total population numbers. The decrease in population numbers shows that the number of rabbits that disappeared without their carcasses being found was higher in autumn 1978 than in winter 1978-79. This was due on the one hand to the lower rate of decay in winter and on the other hand to our attention being drawn to the carcasses by the behaviour of magpies, who were more attracted to carcasses in winter than in autumn.

First, we examine whether the catching procedure caused additional mortality. During

Table 4. Number of rabbits that died and causes of death

	a	b	c	d	e	f	g
1978-79 (6,7 ha)							
Sept.-Oct.	44	0	0	3	1	9	31
Oct.-Nov.	93	0	1	17	0	2	73
Nov.-Dec. }	46	1	1	20	0	1	15
Dec.-Jan. }	46	0	1	5	0	2	
Jan.-Feb.	24	1	0	19	0	2	2
Feb.-March	22	2	0	8	1	11	0
1980-81* (3,5 ha)							
Sept.-Oct.	3	1	1	0	0	0	1
Oct.-Nov.	12	1	0	0	0	0	11
Nov.-Dec.	12	1	0	0	0	0	11
Dec.-Jan.	9	0	0	0	0	2	7
Jan.-Feb.	6	0	0	0	0	0	6
Feb.-March	4	1	0	0	0	0	3
* 1979-80 (no carcasses or remains found).							
a = estimated total number of deaths at the study site, b = trap or ferret, c = myxomatosis, d = stoat, e = fox, f = carcass found, cause unidentified, g = a-(b to f) missing.							

the three years of the study 9 rabbits were found dead in traps (table 5). From the study of the warden's game bag we know that the lethal minimum body weight of adults is around 1100 g (WALLAGE-DREES 1986: fig. 5). Therefore, we expect that rabbits of about this weight or less, if they had not been caught in a trap, would have died from starvation. In two cases, two rabbits were found together in the same trap. This could have been responsible for the death of one of them, but because of the small number involved, this was only a minor addition to deaths from natural causes.

Table 5. Rabbits found dead in live-traps 1978-1981

Date	Body weight (g)	Comments
2-03-1978	860	
9-02-1979	1225	myxomatosis
23-02-1979	1150	
23-02-1979	1100	
21-03-1979	890	
16-09-1980	930	2 rabbits in one trap, one dead
13-11-1980	950	
3-03-1981	1280	2 rabbits in one trap, one dead
03-04-1981	1380	weight loss 240 g since 15-03

Diseases and parasites

Rabbits caught in live-traps did not manifest any symptoms of disease, except for myxomatosis. Rabbits shot in another part of the reserve and dissected had intestinal parasites, especially *Graphidium strigosum* and *Taenia* sp. These rabbits did, however, seem to be in good condition. Only one out of 175 rabbits showed symptoms of liver coccidiosis.

Few rabbits with symptoms of myxomatosis were found (table 4). Other evidence also indicated a low rate of mortality from myxomatosis. Over the three years of the study, 29 animals on the study site were seen to have myxomatosis: 23 of these were juveniles and 6 were adults. At least 10 of the rabbits are known to have recovered. Myxomatosis occurred mainly at the end of summer (table 6). Nestlings may die from myxomatosis in spring without showing symptoms (FENNER and RATCLIFFE 1965). In this study causes of death of nestlings were not assessed.

Starvation

The chance of capture was higher in rabbits that required more food (table 2). Therefore, if there had been starving rabbits in the study area, they should have been caught. In the winter of 1978-79 three of the 'trap deaths' could be attributed to starvation. In this year we observed that rabbits were less alert: another sign of starvation.

In 1980-81 we did not see any evidence of starvation. The weight changes of ten rabbits that disappeared during December-February, and were assumed to have died, were known up to the time of disappearance. These had all been positive (+0.66 to +5.66 g/day). The

Table 6. Number of rabbits on the study site seen with myxomatosis

	1978-79	1979-80	1980-81
September	7	0	1
October	2	0	0
November	2	0	0
December	1	0	0
January	0	0	1
February	0	0	0
March	0	0	0
April	0	1	1
May	0	1	1
June	0	1	-
July	1	3	-
August	0	6	-

comparable figure for rabbits who were observed to be alive in March was -1.10 to $+5.40$ g/day, ($n = 13$). This does not suggest that starvation was a cause of mortality in this year.

Predation

Predation is almost always elusive and hard to measure. The number of rabbits caught by predators can only partly be deduced from table 4. Full-grown rabbits in the coastal dunes were eaten by fox, polecat, stoat and feral cat, and the first three species were seen in the study area. Large numbers of rabbits killed by stoats were found in 1978–79 (table 4, column d). In addition, many of the carcasses of which the condition did not allow determination of the cause of death (table 4, column f) may also have been killed by stoat. Magpies often found the carcass and ate what was left.

In November and December 1978 we found 15 juvenile rabbits killed by stoats that had not yet been damaged by magpies. Their mean weight (\pm s. e.) was 1380 ± 45 g. When we simulated the wounds to rabbits caused by stoats we concluded that an average of 40 g of flesh were eaten. Adding this eaten part gives a converted mean weight of the juvenile rabbits of 1420 g. The mean weight of juveniles in the warden's game bag for the same months was $1450 \text{ g} \pm 25$ ($n = 64$). During this period only one adult rabbit was found killed by a stoat. This suggests that stoats take healthy, but inexperienced rabbits. Stoats may have had no other choice, however, because there were no weakened rabbits present at this time of year. By taking healthy prey the stoat could be a factor influencing rabbit population density.

Polecat kills were not found, but may have been included in the figures for the stoat. A polecat might drag a full-grown rabbit away from the spot where it was caught, but only in the unfenced plots. The same applies to the cats and foxes. Feral cats were scarce in the Dune Reserve. Foxes are known to carry away their prey and bury it, so reducing the chance of finding the remains of fox kills. Carcasses with the head severed or buried were attributed to foxes. Such prey remains were found only twice during the study (table 4, column e).

The number of rabbits caught by foxes were assessed in the following way. MULDER (1985b), who studied the fox in the same dune reserve, estimated that rabbits constitute 90 % of the weight of the diet of foxes. A fox needs 350–550 g (LLOYD 1980) to 480–700 g (NIEWOLD 1976) of food per day. An average (juvenile) rabbit weighed around 1500 g (WALLAGE-DREES 1986). Therefore, one rabbit and some other prey may provide a fox with food for two days. Fox territories in the NHD, on average, covered 165 ha and contained three adult foxes and their young at years of high fox population density. In 1980 they usually contained two adults. Here we calculate the situation at maximum fox density. Assuming that from September until December three adult and three full-sized young inhabit a territory, and that from 1 December the young start to disperse, we might expect 6 foxes/165 ha from September through November and 4 foxes/165 ha from December through April (MULDER 1985a). Their minimum food requirement would then be: 90 rabbits/165 ha per month during Sept.–Nov., and 60 rabbits/165 ha per month during Dec.–April. They might waste food in autumn, but it was assumed not in winter.

Foxes were expected, therefore, to remove one or two rabbits per month over the whole of the three plots of the study in 1980–81; a small loss compared to total rabbit numbers at that time (table 3).

During the study period there was a change in the populations of predators. From spring 1979 onwards, stoats became rare in the whole dune reserve. Foxes have lived in the Reserve since 1968. Their numbers increased up to 1981, after which they remained constant (J. L. MULDER pers. comm.). The increase of the fox population may explain why so few rabbit carcasses were found after spring 1979 (table 4): foxes eat carcasses as well as live prey and both types of food are carried away and hidden.

The impact of the stoat was quite high during the winter of 1978–79. Rabbits weakened by food shortage might have been more susceptible to predation, but the apparently greater effect could have been due partly to the fact that we noticed the carcasses sooner in winter than in the autumn.

With the fall in stoat numbers in spring 1979, predation pressure on rabbits decreased.

The experiment with supplemental feeding

In 1980–81, rabbits in plot 5 were given additional food, but this did not reduce winter mortality (table 3).

Table 7 gives the change in body weight of rabbits that were caught at least twice. In plot no. 5 both adults and juveniles showed a weight gain during autumn and winter, but in the untreated plots, adults lost weight over both periods, and juveniles only gained weight during autumn. All differences between treated and untreated plots were significant, even for the juveniles in autumn. Juveniles supplied with extra food gained more weight than did juveniles in the untreated plots.

One effect of supplemental feeding was that young were born in this population weeks ahead of the usual start of the reproductive season (WALLAGE-DREES 1983). Only three of them emerged, apparently because the conditions in February and March are too harsh for nestlings or suckling does. The ones that emerged had a low growth rate (table 10).

Table 7. Change in body weight in control plots, and in populations supplemented with food (g/day \pm s.e.)

	n	1 Sept.–30. Dec. 1980	n	15 Dec. 1980–6 March 1981
Adults plot 2, 6 and 7	5	-1.3 ± 1.6	4	-1.7 ± 0.8
Adults plot 5 ¹	5	$+3.5 \pm 0.9$	0	
		$t = 3.78, p < 0.05$		
Juv. plot 2, 6 and 7	12	$+2.8 \pm 0.1$	6	-0.9 ± 1.2
Juv. plot 5 ⁺	8	$+3.6 \pm 0.4$	4	$+4.9 \pm 2.3$
		$t = 4.42, p < 0.05$		

¹ Experimental plot: supplementary feeding during October–March.
n = number of rabbits that were caught twice or more in the period.

Productivity

Litter size

The factors which contribute most to a high rate of population increase are early maturation, large litter size, high littering rate and high survival rate of the young.

In 1978 the mean litter size of 34 litters in stops was 5.0 ± 0.2 . Litter size increased from spring to summer (fig. 2) as described by the regression equation for March 21 to May 17: $Y = -0.4 + 0.05X$, $r = 0.478$, $p < 0.005$, where Y is the litter size and X is the birth date as day of the year.

In 1979, 10 stops were found before June. The correlation of litter size with time was not significant. Litter sizes were smaller in 1979: mean litter size was 4.1 with a mean birth date of April 24. On that date the expected litter size for 1978 would have been 5.3.

In 1980 and 1981 three and zero stops were found, respectively, thus mean litter size could not be determined. The mean litter size in utero from 10 rabbits shot in February and March 1981, with an expected mean birth date of about April 1, was 4.4. This was in the range expected from the regression formula for 1978.

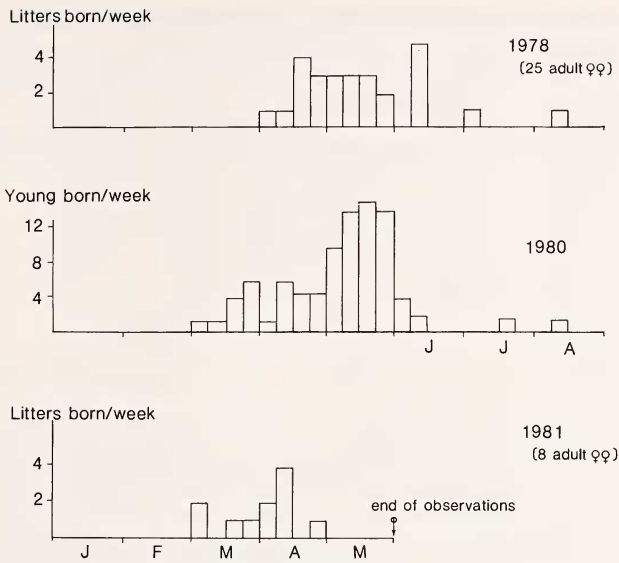


Fig. 3. Number of litters or young born per week in the study area

Table 8. Frequency of age cohorts of juveniles in the game bag in 1978, 1979 and 1980
Totals of September plus October

Month of birth	1978	1979	1980
June	7	45	13
May	27	69	41
April	53	70	36
March	28	16	25
February	8	4	10

Two-sample test Kolmogorov-Smirnov
 1978 vs. 1979 $D = 0.283$ $p_2 \ll 0.001$
 1979 vs. 1980 $D = 0.182$ $0.001 < p_2 < 0.01$
 1978 vs. 1980 $D = 0.156$ $p_2 = 0.05$

Development of the vegetation

The availability of food during the breeding season is shown by the height and cover of the two main plant groups (table 9). The quantity of plant material increased from 1 March, and then decreased before mid-June, particularly in the quantity of dicotyledons which offer the best quality food. As the average height of the plants continued to increase over this period, this decrease seems not to have been caused by rabbit grazing.

Growth rate

The weight of young rabbits caught more than once were plotted against time. For nestlings and young from 200 to 1000 g the increase in weight was arithmetic (table 10). A relationship using the logistic form of the equation failed to improve the correlation. The

Table 9. Relative biomass of the vegetation during the breeding season 1980

Date	Dicotyledons			Monocotyledons		
	Cover	Height (mm)	c × h	Cover	Height (mm)	c × h
13 Feb.	0.10	12	1.20	0.71	19	13.49
27 Feb.	0.14	8	1.12	0.83	17	14.11
10 March	0.11	8	0.88	0.83	22	18.26
24 March	0.13	9	1.17	0.84	22	18.48
7 April	0.15	8	1.20	0.95	22	20.90
21 April	0.24	17	4.08	0.96	18	17.28
11 June	0.02	22	0.44	0.63	19	11.97

c × h = relative biomass.

Table 10. Growth curves of young rabbits

A. Growth curve of nestlings between day 10 and 21 1978 only BW = 22.3 + 8.9 t, n = 15, r = 0.94			
B. Growth curve of young between day 21 and 93 BW = 42.5 + GRt			
year	n	GR	r
1978	18	10.0–11.2	0.98
1979	—		
1980	26	9.4– 9.8	0.99
1981	47	8.6– 9.0	0.98
born in the usual season			
1981	3	7.6– 8.4	0.80
born in Jan. in plot 5			

n = number of individuals that were caught repeatedly and weighed, BW = bodyweight in grams, GR = 95 % confidence interval of the linear growth rate in g/day, t = age in days, r = correlation coefficient

growth rates found in this study are within the range of growth rates reported in other studies (table 11). Those from the young in the population receiving supplemental food that were born in January, much earlier than usual, were comparatively low.

Survival

The survival of young in different cohorts (born in different months of the year) was assessed from the composition of the game bag. Table 12 gives the frequencies of occurrence of age cohorts in the game bag and in the study site as a whole. In 1980–81 there was no significant difference in survival rate between young born early (i. e. March–May) or late in the season (i. e. June–July).

Table 11. Growth rates in different countries

Country	Author	Growth rate (g/day)
England	SOUTHERN (1940)	9.6
New Zealand	TYNDALE-BISCOE and WILLIAMS (1955)	10
Australia	DUDSZINSKI and MYKYTOWYCZ (1960)	6–11
	DUNNET (1956)	9.8
	DUNSMORE (1971)	8–10
	MYERS (1964)	10–11
	MYERS and POOLE (1963)	10–12
	PARER (1977)	10
	PARER and FULLAGAR (1986)	9.1
	WHEELER and KING (1985)	10.5
	WOOD (1980)	9.6–10.5

Table 12. Survival rate of young born in different months

12A. Frequency of age cohorts (young with different months of birth) in the monthly game bag of 1979

Lens weight mg	Sept. Cohort	n	Oct. Cohort	n	Nov. Cohort	n	Dec. Cohort	n
92-114	June	33						
115-132	May	54	June	12				
133-147	April	47	May	15	June	3		
148-160	March	9	April	23	May	5	June	4
161-172			March	7	April	7	May	17
173-182			Feb.	4	March	9	April	11
183-190							March	7
Total n		143		61		24		39

June cohort shot in September vs. June cohort in December:
 $\chi^2 = 2.37$ n.s.

Young up to 3 months seldom appear in the game bag (MYERS 1971). The July and August cohorts that appeared in October, November and December are neglected.

12B. Survival of age cohorts in the study area 1980-'81, plot 2, 6 and 7

Month of birth	n in Sept. 1980	Survival (%) till March 1981
March	5	20
April	14	36
May	7	29
June	0	
July	5	20
August	0	

Fisher exact probability test for March + April + May vs. June + July + August: $p = 0.54$, n.s.

Discussion

Population density

Occurrence of food shortage in autumn and winter

In the field it was impossible to assess the cause of death for every individual. It is assumed here that rabbits that were not seen again or recaptured at the site any more had either died from disease or starvation inside the burrow, or had been carried away after predation.

There were no indications of diseases impairing survival, except for some myxomatosis in August and September during each year. Myxomatosis manifests itself only in spring and autumn and is no longer a major factor in determining the number of rabbits.

Evidence of the influence of food shortage on mortality was gathered in several ways: by assessing the condition of rabbits in wintertime (described in WALLAGE-DREES 1986), by assessing the quality of the available food in winter (WALLAGE-DREES and DEINUM 1987) and by providing supplemental food (this study).

The condition of the rabbits in the study area was assessed by examining live rabbits caught in traps (table 7) and rabbits shot in the dune reserve outside the study area (WALLAGE-DREES 1986). Both data sets showed the same pattern: in all winters there was a decrease in weight, especially among juveniles. Only in the cold winter of 1978-79,

however, starvation did occur. In the other winters very few individuals showed signs of starvation.

WALLAGE-DREES and DEINUM (1987) showed that from December 1980 till March 1981 digestibility of the food was below the maintenance level.

Supplemental food given to one fenced-in population in 1980–81 did not change the mortality rate. This indicates that mortality rate in years with ‘normal’ weather was determined by causes other than food shortage.

It should be realized that the level of the food supply itself is not constant. It changes stochastically with the weather and is influenced by the actions of rabbits, who deplete it at high density, but on the other hand increase its quality by promoting dicotyledons through their grazing (GILLHAM 1955).

During the study widely different weather conditions occurred. High mortality in the long winter of 1978–79 reduced numbers to a low level. In the following years, population density increased, but did not return to the pre-1979 level (table 3). Nevertheless, in 1980–81 a decrease in mean weight occurred in winter and the quality of the food was low.

Predation in autumn and winter

GIBB et al. (1978) found that rabbits in New Zealand hardly ever experienced food shortage because predators kept their numbers below the food limit. We will discuss under what circumstances predators have this impact on rabbits, and whether these are present here.

For vertebrate predators the following characteristics of the ecosystem are mentioned (ERLINGE et al. 1983):

- a. a rich supply of alternative prey sustaining a high and constant predator density. For example for foxes in Sweden, ERLINGE et al. (1983) say that “their diet contained a high proportion of voles in autumn-winter and a low proportion in summer”.
- b. availability of prey for most of the year. GIBB et al. (1969) mention a year-round breeding and hence year-round availability of young rabbits.
- c. a heterogeneous environment where the prey moves through habitats less suitable for them where they are vulnerable to predators (WOLFF 1980).

GIBB et al. (1969) consider characteristic (b) combined with an effective predator like the cat to be sufficient explanation for regulation of rabbit numbers below the food limit.

The main predators in the coastal dunes were the stoat and the fox. Feral cats were rare. The change in the predator population, from stoat plus fox to fox only, occurred at about spring/summer 1979. The decrease of the stoat population could be due to food competition with the fox, especially in the early spring of 1979, when the number of rabbits was low. Also, direct predation by fox on stoat may be involved (cf. ERLINGE 1983).

The decrease in stoat numbers led to lower predation pressure on rabbits. The number of rabbits/ha estimated to be taken by foxes was lower than the number taken by stoats (table 4). Stoats take only healthy animals, foxes both healthy and diseased ones (J. L. MULDER, pers. comm.).

Foxes behave as generalists, even though in the dunes rabbits were their main food. Their numbers are regulated by territorial behaviour and the density of breeding vixens is similar from year to year (ERLINGE et al. 1983; SCHANTZ 1984; J. L. MULDER, pers. comm.).

It is not the absolute number killed but the mortality rate inflicted when the prey population cannot compensate by lowering mortality rate from other causes, in this case the food supply, that is important for the impact of a predator on the dynamics of its prey. So, mortality in late winter has the largest impact (ERRINGTON 1946; NICHOLSON 1954; SOLOMON 1969). The 1 rabbit/ha per month taken by foxes in February could have some influence on a population density of about 7 rabbits/ha (table 3).

Looking again at the characteristics mentioned before

- ad a.: foxes apparently hardly take any alternative prey in the coastal dunes.
- ad b.: there is a short breeding season on the rabbit, young rabbits are only available from mid April–September.
- ad c.: it seems that the whole dune system can be considered a refuge or optimal habitat for rabbits in the sense meant by WOLFF (1980). There is no suboptimal habitat where rabbits disperse at high densities.
- In conclusion, in this study rabbit numbers grew to the point where they were limited by food and predation did not regulate rabbit numbers.

Recruitment

Intrinsic factors: influence of density on recruitment

Average litter size was 5, which was within the range expected in high-density populations (LLOYD 1970). Litter size is strongly related to body weight of the does (BRAMBELL 1943; POOLE 1960). The lower body weight of the does in this study in 1979 explains the smaller litter size in this year.

The low littering rate found in this study seems to be related to population density: it was higher in 1980 than in 1978.

The short breeding season in the study populations can be interpreted as an intrinsic response to high population density or as a response to low food quality in summer.

The beginning of the breeding season (presence of pregnant females) in February or March is determined by the availability of good quality food (WALLAGE-DREES 1983).

What determines the end of the breeding season? Usually the end is near 1 May. After that date few females become pregnant any more. For an explanation for the timing of the end of the breeding season we may consider the fact that there was a difference in the ending of reproduction between 1979, when reproduction continued or was resumed in summer, and 1978 and '80 when reproduction finished earlier.

Many authors from different countries in the northern and southern hemispheres mention that rabbits show a depression in fertility before or at summer solstice, with sometimes resumed breeding in autumn. They consider this an adaptation to arid conditions in the ancestral mediterranean homelands of the rabbit (BRAMBELL 1943; HUGHES and ROWLEY 1966; LLOYD 1970; MCILWAINE 1962; PARER 1977; POOLE 1960; ROGERS 1981; SORIGUER and ROGERS 1981; WOOD 1980). HAMMOND (1965) found that even in domestic rabbits (when they are on a low plane of nutrition) summer anoestrus occurs.

It is hard to believe that this ancestral pattern would still exist in an animal that has been in our temperate coastal climate at least since 1250 A.D. (RENTENAAR 1978). Individuals are supposedly selected for maximum reproductive value. There is individual variation in littering frequency, that, if genetically determined, should enable natural selection to act.

There is evidence for the influence of density, and also for that of food quality on the breeding pattern. In this study summer anoestrus occurred only in 1978 and 1980, years with a high population density, but not in 1979 when population density was low (fig. 3, tab. 8). A similar influence of population density was also found by LLOYD (1970). The growth rates of the young found in this study were within the usual range. So, in spring and summer there seems to have been sufficient food of high quality. Young born at summertime had the same chances of survival as the others (table 12) hence the number of offspring from an individual would increase if that individual continued breeding as long as possible. However, the high survival rate of late-born young in 1979 might have been caused by the fact that they experienced less than usual food competition from the early-born young (GARDON 1986).

It is possible that longer breeding would lower the survival chance of the doe and hence her chance to reproduce in the following spring. This has not been measured in our study.

However, rabbits are known to be able to breed much longer than three months, even in our temperate climate (BRAMBELL 1943).

Population density affects food quality. At a low population density (e. g. in 1979) rabbits have more choice of food plant and can enhance the quality of their diet.

Generally, the concentration of protein in grasses is lowest in June/July and increases again in August/September (MCNEILL and SOUTHWOOD 1978). Also the species composition of the vegetation changes unfavourably after the end of April (table 9).

Recently BOYD (1986) described that the administration of 6-methoxybenzoxalinone (6-MBOA) to rabbits can prevent reproductive regression when the breeding season would normally end. A precursor of 6-MBOA is especially prevalent in the growing shoots of grasses. A regrowth of the vegetation often occurs in August/September.

So intrinsic responses of production size to population density do occur, but they might to a large extent be the results of the interaction between rabbit and vegetation.

Recruitment into the autumn population

After the decrease in population numbers in winter 1978–79, the longer breeding season could not compensate for the later start of breeding and smaller litter size that also resulted from the harsh weather conditions. Recruitment was not sufficient to allow recovery of the population from the extra mortality in that winter.

Interestingly, COOKE (1981) found in S. W. Australia that rabbit populations needed two years to recover from a drastic change in density and the same is mentioned by SHEAIL (1971).

The rate of increase of the population might have been slowed down by predation of foxes on nestlings and young (TITENSOR 1981).

Conclusion

Although predation is important and may slow down the rate of increase in rabbit population numbers, the potential maximum density reached by the population was set by the quantity and quality of food. The availability of food varied stochastically with the weather. In some years, e. g. 1978–79, severe food shortage caused a major reduction in population numbers. In other years, e. g. 1979–80 and 1980–81, rabbit densities were not curtailed by food shortage. In this latter case, low rabbit numbers and abundant food may give the impression that rabbit numbers are kept below the limit set by the food supply by other factors. However no mechanisms would prevent the population from rising to its food limit again.

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Zusammenfassung

*Der Einfluß des Nahrungsangebot auf die Populationsdichte von Kaninchen, *Oryctolagus cuniculus* (L.), in einem niederländischen Dünengebiet*

Die Populationsdichte von Kaninchen wurde in einem gemäßigten maritimen Klima hinsichtlich folgender Frage untersucht: Wird sie durch Selbstregulation kontrolliert, durch Feinddruck und Krankheit, oder steigt die Individuenzahl bis zu einer durch das Nahrungsangebot bedingten Höchstgrenze? Die Studie wurde an mehreren Beobachtungsstellen in einem Dünenreservat an der

Küste durchgeführt. Im Herbst und Winter wurden in einem Experiment zusätzliche Nahrung angeboten. Der strenge Winter 1978–79 führte bei vielen Kaninchen zum Hungertod, aber in den folgenden Jahren nahm die Populationsdichte wieder zu, erreichte jedoch nicht die durch das Nahrungsangebot ermöglichte Höchstgrenze.

Die Wurfrequenz pro Jahr war nicht hoch, wahrscheinlich beeinflusst durch die große Populationsdichte. Die Länge der Fortpflanzungssaison wurde bestimmt durch die Wechselwirkung zwischen Populationsdichte und Nahrungsqualität. Erwachsene Kaninchen wurden von Füchsen und Hermelinen erbeutet, manchmal auch von Katzen oder Iltissen. Feinddruck und andere Mechanismen, die möglicherweise für eine Regulation der Bestandsentwicklung verantwortlich sein könnten, waren nicht stark genug, um die Zahl der Kaninchen permanent unter der durch das Nahrungsangebot bedingten Grenze zu halten. Die Gründe dafür werden besprochen.

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